Respecting the relative efficiency as protecting agents of the Nipher jacket and the Wild fence, experimental observations have been, and are apparently still being, conducted in Russia, a country, be it noted, where, owing to the large quantities of snow that fall during the colder months of the year, the sources of error in rain-gauge records through wind assume greater magnitude than they do, for instance, in England, where the winter precipitation consists largely of rain. It may be said that, while the Nipher protector is generally well adapted to its purpose for ordinary situations of rain-gauges, it may be with advantage replaced by the fence enclosure in the case of gauges which are unduly exposed to the full force of the wind in unsheltered locations. If the accuracy of the Wild fence be taken as 100, that of the Nipher jacket may approximate to 100 in more sheltered positions, but may be as low as 80 or even lower in such as are quite open to the violence of the wind. It should be added that a Nipher gauge ought to be fitted with some form of heating apparatus adequate to prevent accumulations of snow in winter upon the protecting jacket, from which into the rain-gauge portions of such accumulated snow are liable to be blown.

This brief abstract of the chief methods of diminishing or eliminating the wind error due to rain-gauges would be incomplete were it omitted to mention a process of calculation [1] by which the rainfall figures for a sufficiently long period, as indicated by a gauge at a place which suffers undue exposure to the wind in comparison with another gauge in the neighbourhood, say a few miles distant, at a more sheltered spot that may be regarded normal, may be corrected. The method depends upon the relation subsisting between the amounts of discrepancy in the records of two such gauges during periods of rain and of snow. If the rainfall for a specified time at the sheltered station be represented as 100, and that at the exposed station as $100-A$ for periods of rain and $100-A-B$ for periods of snow, the equation $K=\frac{x+A}{B}$, when solved for x, affords the correction required. The value of K, which for a few localities in Germany has been found to range from 0·13 to 0·22, must be empirically determined for a particular district by establishing two similar rain-gauges close together, or, if possible, side by side, one of which is fitted with an efficient wind-protection contrivance, the other being left free; for a pair of gauges in such close proximity x may be considered to vanish, so that K becomes $=A/B$. The value of K for the locality being thus found, x is solved $=KB-A$, which will, of course, be a *plus* or *minus* quantity according as the true rainfall is slightly greater or less at the exposed than at the sheltered station. This method of calculation, which is applicable in many instances, has been tested by another more direct one involving anemometer readings, whereby the measured quantities of precipitation could be reduced to equal mean wind velocities, and as the two have given most concordant results, it may be concluded that the one briefly delineated above is correct.

Thus at Karzig, in Neumark, the rainfall at an open, wind-swept spot on the outskirts of a forest, though indicated by a rain-gauge as considerably less than that of a glade more than 2 kilometres distant, was found by both processes of calculation to be actually 2 per cent. greater.

To summarise the contents of this article:—

(1) Experimental observations extensively carried out during the nineteenth century in many countries have established the fact that in the measurement of rainfall errors of considerable magnitude accrue from the presence of the rain-gauge during the prevalence of wind, and point to the conclusion that such errors arise from the eddying or rebounding of wind about or from the mouth of the rain-gauge.

(2) The readings of a rain-gauge in a free, open situation may be corrected by means of a method involving their comparison with those of another similar gauge placed at twice the height above the ground.

(3) The most efficient wind-protection contrivances for rain-gauges are the Nipher jacket and the Wild fence enclosure; the latter, though more accurate and advantageous in special circumstances, is generally less used than the former.

(4) The corrected rainfall for a sufficient length of time of a wind-swept spot may in many instances, if the rainfall for the corresponding period of a sheltered spot in the same neighbourhood, say a few miles distant, be known, be determined by means of an equation involving as known data (*a*) the relative amounts of discrepancy in the records of the gauges at the two places during periods of rain and of snow; (*b*) an empirically determined constant K.

L. C. W. BONACINA.

[1] *Meteorologische Zeitschrift*, Band xxiii., 1906, s. 444, "Wald und Niederschlag in Westpreussen und Posen und die Beeinflussung der Regen und Schnee-messung durch der Wind," von J. Schubert.

RECENT DEVELOPMENTS IN THE THEORY OF MIMICRY.[1]

THE remarkable resemblances that exist between certain insects belonging to widely different orders have long been known to naturalists. Wasps and hornets are imitated by the "clear-wing" moths, the resemblance being so close that it has sometimes deceived for the moment a skilled entomologist. Certain two-winged flies that inhabit the nests of humble-bees are scarcely to be distinguished from their hosts, and the handsome Xylocopas, or carpenter-bees, familiar objects in the tropics, are deceptively copied by two-winged flies found in the same regions.

But it is not only the bees and wasps that are so imitated, nor are the imitating insects to be found only in the ranks of moths and flies. An ichneumon fly in Borneo, belonging to the same order as the bees and wasps, though not in the same sense a stinging insect, is closely copied by a Reduviid bug.

Other instances are numerous. So long ago as the year 1836, the French entomologist Boisduval directed attention to the extraordinary resemblance that exists between certain butterflies which are not at all closely related to each other, belonging, indeed, to groups which are widely distinct. One of these butterflies is a member of the Danainæ, a group of which we have no resident representative in this country; a second is nearly related to our familiar "swallow-tail" of the Cambridgeshire fens; while the third is a Nymphaline, not far removed from our British "White Admiral." The structural differences between these butterflies show the want of real affinity between them in spite of their superficial resemblance. The "cell," for example, of the hindwing is open in the Nymphaline, while in the other two it is closed by a transverse vein. This illustrates the point that these resemblances affect only obvious characters; they are independent of affinity or blood relationship, and leave untouched such morphological features as do not readily meet the eye.

An insect thus resembled by another is spoken of as its "model," the imitating insect is called a "mimic," and the combination of model and mimic or mimics is known as a "mimetic pair" or "mimetic assemblage," as the case may be.

What is the meaning of these resemblances? Many of them were well known to the older naturalists, who, however, had nothing to offer by way of explanation but vague talk about "repetition" and "analogy" in nature. The well-known entomologists Kirby and Spence got so far as to suggest that in some cases the resemblance might be of advantage to the mimic, but in their day it was not likely that the subject should be treated from the evolutionary point of view, and the first really scientific explanation of the matter was given by Bates on his return from his famous visit to the Amazon, now nearly fifty years ago.

Bates had observed that in these cases of deceptive resemblance between butterflies, one member of the pair or of the group was often characterised by abundance of individuals, while the whole group was marked by slowness of flight, conspicuousness of appearance, and immunity from the attacks of insect-eating birds. On these grounds he put forward the suggestion that the mimicking species enjoyed protection from attack by their

[1] An evening discourse delivered at the Leicester meeting of the British Association on August 5 by Dr. F. A. Dixey.

resemblance to their more abundant models, the immunity of which, he thought, was due to the possession of some distasteful quality—probably a scent or flavour disliked by the birds.

Accepting Darwin's view of evolutionary process, he attributed the formation of these resemblances to the accumulation by natural selection of variations in the mimicking species that happened to point in the appropriate direction; so that these mimics had gradually put off the general aspect of the group to which they properly belonged; and had become more or less completely assimilated in outward appearance to the members of an entirely different assemblage; thus sailing, as it were, under false colours, as if a peaceable merchantman were to disguise itself under the rig and ensign of a man-of-war. This is the well-known Batesian theory of mimicry. It was at once, and cordially, accepted by Darwin; while the array of facts from South America on which it was based was soon afterwards shown to be paralleled by corresponding phenomena in the Malayan Archipelago and in South Africa. This was the work of two great naturalists happily still with us, Alfred Russel Wallace and Roland Trimen.

An objection was raised in early times to Bates's view on the ground that it was difficult to account for the first advances towards the formation of a mimetic pattern. This objection was felt in some degree both by Darwin and by Fritz Müller, of whom we shall hear more presently. Darwin and Müller thought that the objection might be met by supposing a considerable original likeness between mimic and model; it can, however, quite easily be shown from forms actually at present existing that a complete series of gradations may occur between the ordinary type of a mimetic genus and its very distinct-looking model or models. The transitional forms, even those exhibiting the earliest stages of mimetic assimilation, are evidently able to maintain themselves (how they do it we shall see later), and they in many cases form a perfect succession of links between extreme forms of the utmost divergence in aspect. Hence it is unnecessary to suppose that a considerable initial resemblance must exist between mimic and model, while the initial stages of the mimetic pattern, however we are to account for them, are not only theoretically possible, but are found to be in actual existence.

The beauty and simplicity of Bates's theory commended it strongly to public acceptance, and it is probable that to this day, when the subject of mimicry is mentioned, it is the Batesian theory that presents itself to most people's minds.

But notwithstanding the immense value of Bates's contribution to knowledge, it is now evident, as we shall see, that he only touched the fringe of a great subject, and that a much wider view is necessary before the facts observed by him, and subsequently by others, can be fully explained.

Those who read Bates's classical paper cannot avoid remarking that he himself was not thoroughly happy about all the facts there recorded. He directs attention to the circumstance that not only do the mimics resemble their models, but that the models themselves often show an extraordinary resemblance to each other. He speaks of "a minute and palpably intentional likeness which is perfectly staggering."

To take an instance: two species of the Ithomiine genus Dircenna, *D. epidero* and *D. rhaeo*, structurally distinct, but almost indistinguishable on the wing, were noted by Bates as being always found together where they occur in the Amazonian region. A moth, *Hyelosia tiresias*, was regarded by Bates as a mimic of *Dircenna epidero*, but it did not escape him that his theory failed to account for the resemblance of the two Dircennas to one another, the subfamily Ithomiinæ, to which they belong, being on good grounds supposed to be generally distasteful. The difficulty becomes still greater when it is realised that not only members of the same presumably distasteful genus, but also members of different genera, all with the same habits and denizens of the same region, bear the same extraordinary likeness to each other. There are, for example, some twenty species of Ithomiines, belonging to no less than seven different genera, all with the same, or very nearly the same, external appearance. But this is not all, for the same mimetic assemblage will be found to include, not only these Ithomiines, but also butterflies belonging to the group of Danaines (genus Ituna) and Pierines (genus Dismorphia), as well as moths of the two widely separated groups of Hypsidæ and Castniadæ, all with a common facies.

If it were merely a case of resemblance between two or more species of the same genus, such as the Dircennas that have just been mentioned, we might be tempted to say that the resemblance was merely due to affinity, and to explain, as Bates did, the circumstance of the constant companionship of the two species by appealing to the "social and gregarious instincts of the group." When, however, we see that not only Dircennas, but Ithomiines generally, Danaines, Pierines, and moths all come into the same mimetic assemblage, the explanation from affinity breaks down. Affinity, no doubt, may help mimicry, but there is no necessary connection between the two. Some members of the company are closely related; others are widely distinct. Bates himself saw clearly enough that his theory of one distasteful and immune form sheltering others which would be attacked if detected would not apply to cases of this kind. If all the species but one of a "homœochromatic" group are to be considered as edible mimics, we should have to account for the fact that they vastly outnumber the model, in which case the mimicry would be more harmful to the model than beneficial to themselves; we should also have to face the improbability of one species of a genus being distasteful and immune, while other species of the same and allied genera were edible and liable to attack. It was plain that the distasteful models did really imitate each other, but why?

All that Bates could do in the face of this difficulty was to fall back, somewhat doubtfully, on the hypothesis of some local or climatic cause acting equally upon the forms of different groups, and in some unexplained way bringing about this strange resemblance between them. In this supposition he was for a time followed by Wallace.

It is not to be denied that there is a certain plausibility at first sight in this view concerning the direct action of external conditions. It is, for example, a striking fact that the members of a mimetic group of very diverse affinities will, as Bates says, every few hundred miles all change their hue and pattern together, "as if by the touch of an enchanter's wand."

There is a well-marked assemblage of this kind, generally characterised by a pattern composed of the three colours red, yellow, and black. It contains, besides moths, butterflies of many diverse groups, Ithomiines, Heliconiines, Danaines, Nymphalines, and Pierines—in some of the latter the female only taking part in the mimetic cluster, a point to which we shall return later on. The members of this assemblage as it occurs in the northern part of Central America—Guatemala to Nicaragua—present in common a remarkable streakiness of pattern, a feature that makes them easily recognisable among the corresponding forms from other regions of the same continent. Passing on to Venezuela, we find among the geographical races, or, if we like to call them so, the representative species, that there replace the Central American forms, a tendency to the breaking-up of the streaks, and a slight encroachment of the red ground-colour upon the yellow of the apex. In Trinidad there occurs a general paling of the ground-colour, due to an increase of yellow pigmentation, and running, as before, through the entire group. Next, taking the corresponding Guiana forms, we find a further breaking-up of the streaks into spots, and also a general darkening, especially of the hindwings, which gives a most characteristic aspect to the whole assemblage. In East Brazil we have a modification which somewhat recalls the Trinidad facies, though here the yellow streak on the hindwing is better defined, and the black of the apex is less broken up. At Ega, on the Upper Amazon, a curious dark chestnut tinge pervades the group, while in Peru a characteristic spottiness takes the place of the streaky pattern we saw elsewhere, and the apex becomes more uniformly dark. Finally, in Ecuador the streaks have all but disappeared, and even the spots have become almost blocked out by a

dark infusion which now occupies, not only the apex, but also a large part of the base of the forewing, and the whole, or nearly so, of the hindwing. After a little study of some of the typical members of each of these geographical groups, it becomes easy to pronounce, with a considerable degree of confidence, upon the local habitation of a species that we may never have met with before.

If facts of this kind were the only ones with which we had to deal, there might be some justification for adopting the theory of the direct effect of geographical conditions, but it is now incumbent on us to consider whether this hypothesis of common surroundings producing a common aspect will bear further examination. We will take the instance of a group of ant-like insects caught by Mr. Guy Marshall in Mashonaland on one day on a single plant. All were to outward appearance ants; but while the first four were veritable ants, the next two were bugs, and the last was a locustid, belonging, that is to say, to the order of crickets and grasshoppers. If a common environment has of itself produced the ant-like appearance of the bugs and the locust, why has it not done something towards assimilating the points of structure that do not meet the eye? As a matter of fact there is no such approach. In internal organisation each member of the group preserves the exact characters of its own order.

There is a certain ant-like locustid, possibly of the same species as that last mentioned, in which the body of an ant is, as it were, painted on that of the locust. The constriction between thorax and abdomen, real in the ant, is in the locustid only apparent. Can the external conditions which are supposed to have caused the characteristic shape of the ant actually paint a copy of the ant on the otherwise unaltered body of the locust?

Again, there are cases where the supposed external influence must have acted, if at all, as sculptor instead of painter. In a certain ant-like Membracid (an insect allied to our common "cuckoo-spit") the body of the insect is concealed beneath a shield, which grows backward from the fore part of the thorax. This shield or screen, which is quite separated from the body except along one line of attachment in front, is hewn or moulded, so to speak, into the form of an ant, reproducing even the small swelling in the peduncle which is characteristic of some ants of the region that this insect inhabits.

Another instance, probably familiar, but so much in point that I cannot refrain from mentioning it, is that of the immature form of a Membracid found by Mr. W. L. Sclater in Guiana among a number of leaf-cutting ants. The flat green body and brown head and legs of the Membracid make a very fair copy of the ant engaged in its occupation of carrying home the cut leaf, the picture including, not only the ant, but the leaf as well. Ants are avoided by some enemies, though not by all, and in a procession of ants of this kind it is not likely that an enemy, however sharp-sighted, would readily pick out the Membracid from among its leaf-carrying companions. The idea that external conditions can produce in another insect a copy, not only of the ant, but of the leaf which it carries, needs, I think, only to be mentioned to be dismissed.

Looking at the matter from a slightly different point of view, we may take the instance of the wonderful African butterfly *Papilio dardanus*, no very distant relative of our English "swallowtail." The male of this insect is non-mimetic, while the female occurs in three or four different forms, each of which is a palpable mimic of a separate model. On the theory of direct external causes we have to explain why these external conditions have brought about a resemblance between each form of the female and a separate model of different affinities, while these causes have not been able to prevent individuals of the same species from going off in four or five different directions.

The facts here have been questioned, but as all the diverse forms have been found among the offspring of one individual, there is no longer any room for doubt that they are all really conspecific.

We can get more light on the subject if we return for a moment to our assemblage with transparent wings, the assemblage, that is, which contains the two Dircennas, *rhaeo* and *epidero*.

Now if the effect of transparence, which is common to the entire group, had been the direct result of an external cause, we should expect it to have been brought about in all cases by the same means; but whereas in the Ithomiines the transparence is due to an alteration in shape and diminution in size of the minute scales which normally clothe the wing, in the Pierines the same effect is produced by a mere diminution in size, the shape remaining unaltered. The Danaines of the group owe their transparence to a reduction in the *number* of the scales, not to any alteration in shape or in size; while in the associated moths the effect results, not from any change in size, shape, or number of the scales, but from the fact that the individual scales themselves become transparent, and are sometimes set up vertically, so as to let the light pass between them.

In view of these facts, the investigation of which we owe to Prof. Poulton, it is difficult, if not impossible, to imagine any direct agency which will produce the same visual effect by all these different means. The likeness is superficial; the real difference is profound. The common features, if we may so express it, are only meant to be looked at. They must stand in relation to vision of some sort; and to whose vision, we may well ask, if not to the vision of would-be enemies? Natural selection will attain the desired end by any means that come to hand, and these observations of Poulton seem to put every other explanation in this case out of court. If we may be allowed to use, without prejudice, teleological language, we may say that these resemblances have been brought about by natural selection for a mimetic purpose. Any variation, whether in size, shape, number, transparence, or position of scales, which leads in the required direction, will be preserved; and the final result, though to ordinary vision identical in all cases, will bear evidence, on close examination, of the manner, different in each individual case, in which it has been effected.

But, it may be said, many of your instances are simply cases of Batesian mimicry, and for them we can allow the sufficiency of natural selection; it is the other cases which want explaining. This is quite true, but a great point is gained if we have shown that, in many of these cases, neither affinity nor the direct agency of external conditions will account for the facts, while natural selection will do so if only we can find out why it should be an advantage for these distasteful types to form themselves into groups. If we *can* bring both kinds of mimicry under one cause, we are bound to do so. The old logical canon, the "razor of Occam," applies here. "Entia non sunt multiplicanda praeter necessitatem"; in other words, having found an adequate cause for one case of a given phenomenon, we are not at liberty to go out of our way to seek another cause for a second case of the same phenomenon. We must first try if the cause already established will not meet the requirements of the situation.

What we have to do, then, is to prove, if we can, why it should benefit these *distasteful* forms of various affinities to fall into homœochromatic groups, groups, that is, essentially similar in outward aspect. For a long time the key to the puzzle eluded discovery; it was at last found by Fritz Müller.

This admirable naturalist, working, like Bates, in South America, put forward in the year 1879 a suggestion which, when developed into its full consequences, has revolutionised our conception of the whole subject.

His suggestion rested on the assumption (since shown, mainly by Lloyd Morgan, to be correct) that birds have no instinctive knowledge of what forms would be suitable for food and what should be avoided, so that each bird has to gain its knowledge by experience. Hence a certain number of distasteful forms must be sacrificed by each generation of birds until these enemies have learned to leave such forms alone. In other words, each distasteful form has to *pay a tax* for its immunity.

Now if two distasteful species resemble each other so closely that birds or other enemies do not distinguish between them, the disagreeable experience gained by tasting an individual of one species will be applied to the benefit of the other, and so each of the two species will only need to contribute a portion of the tax, instead of

each paying the whole—a consideration which, I think, will go home to most of us. And what is true of a combination of two species will be equally true of a larger assemblage; the greater number of forms that can be got to share the tax, the better for all. Hence the formation of these large "inedible associations," or, as they might be called, Müllerian groups. I do not wish to be understood as saying that the Batesian and Müllerian theories are mutually incompatible. They are *supplementary* to each other, and there is ample room for true mimicry beside or within the ranks of the Müllerian associations.

Though the theory of which I have just given an account is really quite simple, it has never been so generally understood and appreciated as that of Bates. May I, at the risk of being tedious, try to illustrate the relation between the two?

Imagine a large box of sugar-plums, and a schoolboy given *carte blanche* to help himself from it as he likes. Imagine, further, that the sugar-plums are of different colours and flavours, and that some of them are flavoured with an essence which the boy does not like—we will say aniseed. Further, let all the aniseed sugar-plums be coloured pink. The boy will soon find out that the pink sugar-plums are unpleasant to his taste, and *after a trial or two* they will be left until all the others have been disposed of, or, if sufficiently disagreeable, they will be refused altogether. The pink colour is here an *aposeme*, to use Prof. Poulton's term, or the visible mark of a distasteful character.

Suppose a few pleasantly flavoured sugar-plums to be coloured pink like the aniseed sugar-plums. These, if there are not so many of them as to destroy the impression of nastiness associated with pink, will also be left. This represents Batesian mimicry. The few pleasantly flavoured sugar-plums share in the protection afforded by the pink aposeme.

Now for Müllerian mimicry. Let us suppose that there are *two* flavours disliked by the boy, say aniseed and peppermint, and that the sugar-plums with these flavours are coloured pink and green respectively. The boy would have to try both pink and green before he learned to avoid them. Perhaps two of each, two of the pink and two of the green, *i.e.* four in all, would be sufficient to complete his education in this respect; but if *both* kinds of disagreeable sugar-plums were coloured pink, a trial of two only, instead of four, would be sufficient to protect all the rest, of both flavours, aniseed and peppermint, from the boy's depredations. In other words, the tax paid by each would be halved, and so with larger numbers. Hence the advantage of a common aposeme for *distasteful* objects, whether sugar-plums or butterflies.

This illustration refers only to the relation between the two theories. It says nothing, of course, as to the means by which the sugar-plums originally became coloured and flavoured; but what we *have* done is to show the advantage to be gained by Müllerian association, and therefore to supply the required motive power for natural selection.

Müller's suggestion was brought to the notice of British naturalists by Prof. Meldola in the year of its first publication, and in its further developments at the hands of Meldola himself and of Poulton it was accepted both by Wallace and by Trimen, the two naturalists who had done most by their own observations to confirm the validity of the supplementary (though earlier-devised) theory of Bates.

Fritz Müller had spoken chiefly of the resemblance between two butterflies, Ituna and Thyridia, belonging to distinct subfamilies, but it was soon pointed out by Prof. Meldola that the general likeness between members of the same distasteful family groups came easily under the same principle.

In order to appreciate this point fully, let us consider the common European Vanessas, the Peacock, Red Admiral, large and small Tortoiseshells, Camberwell Beauty, &c., several of them familiar objects in our own country. We see at once that though there is certainly a family likeness between them, they are distinguishable from one another at a glance; no one would think of taking one of them for another. Contrast this with a similar group of closely allied species, known to be distasteful, from a part of the world where competition is keen, for instance, the Acræas of Africa. Of these, four or five species may be taken on the same day, looking all alike while on the wing, and practically indistinguishable from one another without close examination. Or take a group of Euplœas, another distasteful genus, from the Oriental region. Here again we may have some five separate species, all quite distinct, but so much like one another that it needs much more than a casual glance to distinguish between them.

These and similar cases were shown by Meldola to be easily explicable on the basis of the Müllerian theory of mutual protection by the adoption of a common scheme of warning colours on the part of inedible forms, and the possibilities of the theory were still further expanded by Poulton, who pointed out that in any given region the fewer independent schemes of warning coloration there were to learn, the better chance there was of the protection they afforded being effective; so that the same simple warning badge, such, for instance, as the alternate black and yellow rings on the body of a wasp, might be employed by insects, like the caterpillars of the Cinnabar moth, which are widely separated from the wasp in point of affinity. The aposeme, or signal to an enemy to keep his distance, may be recognised and obeyed even when hoisted by insects which have little else in common between them. A great part of the significance of the facts that we have noticed depends, of course, on the circumstance that the members of each of these closely assimilated groups inhabit the same geographical areas. We do not find an Eastern Euplœa resembling an American Heliconius, or an Ithomiine from Brazil recalling an African Acræa. As a further illustration of what Poulton has aptly named "synaposematism," or the adoption of a common warning badge on the part of distasteful forms, we may take the wonderfully diverse assemblage that centres round the conspicuous and distasteful beetles belonging to the genus Lycus. This assemblage, in South Africa, contains wasps, Braconids, moths, a bug, and a two-winged fly, besides beetles belonging to three or four different families. I have myself seen several members of this group, heterogeneous in affinity though wonderfully similar in hue and pattern, on or about one tree at East London, in South Africa. Be it remarked that they were all conspicuous insects, and exposed themselves freely, so that there could be no question of a common cryptic coloration. The assemblage, beyond doubt, is mainly if not entirely synaposematic.

We have now reached what may at any rate rank as a preliminary generalisation, that is to say, that the resemblance between distasteful forms is to their advantage, and is an adaptation brought about by natural selection. Following the approved logical method of Mill and Jevons, we ought next to see what consequences are involved in the hypothesis we have formed, and then to make a fresh appeal to the facts for verification or the reverse.

(1) It is obvious that in Batesian, or true mimicry, the advantage is all on the side of the mimic. Experience gained by tasting the mimic would be used to the injury of the model. While, therefore, there is every inducement for the mimic to seek safety by approaching nearer and nearer to the aspect of the model, there is no reason for the model to assimilate itself to the mimic, but rather the contrary.

In a Müllerian association, on the other hand, the benefit is mutual. Each fresh accession to the group is a source of strength, not of weakness. Everything is in favour of the formation of such groups as rapidly and on as large a scale as possible; hence there is nothing to impede, and everything to promote, the free interchange of characters all round, each member being able to act, so to speak, *as both mimic and model*. This, we saw, could not happen in the case of Batesian mimicry.

Now does this interchange of characters, as a matter of fact, ever take place? If it does, it will be, of course, a confirmation of our theory.

One of the most characteristic features in the subfamily of Pierines, or "white butterflies," is the possession of red or yellow spots, streaks, or patches on the underside

of the hindwing, near the base. These marks reach a high state of development in some members of the Eastern genus Delias, and relics of them are to be seen in the common white butterflies of our own country.

Now no one who accepts mimicry at all will be inclined to doubt the existence of a mimetic relation between *Heliconius guaricus* and the Pierine *Pereute leucodrosime.* How has it been brought about? The dark colour and red band are not at all characteristic of Pierines, and have no doubt been copied from the Heliconius; but the Pierine red spots have passed the other way, being taken up by the Heliconius from the Pierine. This, I believe, was the first case of mimetic interchange noticed.

Another instance. White is not an ancestral colour in Heliconius; it *is* ancestral in the Pierines. The Pierine *P. locusta* falls by its undersurface into mimetic association with the group of Heliconius represented by *H. alithea* and *H. galanthus.* The white colour has passed from Pieris to Heliconius; the dark, in great measure, from Heliconius to Pieris.

Much the same has happened in the case of *Heliconius leuce* and the female of *Pieris noctipennis.* These two have undergone reciprocal change. The white comes from the Pieris, the black from the Heliconius.

There is another case where two species belonging to widely separated sections of the same subfamily are in question. The hindwings of the island form of the Pierine *Huphina nerissa* have been drawn away into imitation of the hindwing of *Ixias baliensis*, also a Pierine; while the forewing of the Ixias, leaving the usual aspect of its genus, has been assimilated to the forewing of Huphina.

Another good example of interchange is afforded by the "swallowtail" *Papilio rex* from Uganda, which is in undoubted mimetic relation with the Danaine *Melinda formosa.* The brown at the base of the forewings is a Danaine character adopted by the Papilio; the pale areas at the base of the hindwings are a Papilionine character adopted by the Danaine. Each has in one of these respects acted as a model to the other. The two African genera Mylothris and Phrissura, the species of which form a parallel series of mimetic pairs analogous to the Ithomiines and Heliconiines of tropical America, furnish what is probably another instance of the same phenomenon. For this mutual approach by a process of give and take on both sides, Prof. Poulton has proposed the apt term "diaposematism," the idea of reciprocity being conveyed by the Greek particle "dia."

Let us now look at the working of this reciprocal principle in another direction.

It is well known that where the sexes differ in the extent to which they are protected, whether by power of concealment or by other means, it is almost invariably the female that has the advantage. This was pointed out long ago by Dr. Wallace, and was, no doubt rightly, attributed by him to the fact that the continuance of the life of the female, as the guardian of the early stages of the future brood, was of greater importance than that of the male to the welfare of the species. So we find many cases in which the female alone is mimetic, not the male. Shall we say that "Nature abhors the unprotected female"?

We have already noticed the case of *Papilio dardanus*, with its non-mimetic male, and three or four different forms of female, each form in mimetic relation with a Danaine model.

The case of the Pierine *Leuceronia argia* is in many respects parallel to that of the Papilio. Again we have a non-mimetic male, and several different forms of female, each being in mimetic relation with another butterfly of quite different affinities.

Once more: the female of the Nymphaline butterfly *Hypolimnas bolina* falls into mimetic association with Danaines and with a Papilio, leaving its own male outside the group. It will be remembered, also, that much the same thing occurs with certain of the South American Pierines which we considered in an earlier part of the present lecture.

These instances are sufficient to show the readiness of the female, as distinct from the male, to enter a mimetic combination.

Bearing these facts in mind, when we look at such a combination as that of *Papilio iphidamas* with *Euterpe approximata*, we shall have little or no difficulty in recognising that here we have an analogous case. The sexes of the Euterpe (a Pierine) and the female of the Papilio all resemble each other, while the male of the Papilio stands apart. We have just seen how readily the female of a given species may be drawn away into a mimetic relation apart from its own male, and we have every reason to suppose that the same has occurred here, only that in the case of *P. dardanus*, *L. argia*, and *H. bolina* the pull has been mainly or entirely away from the *dardanus*, *argia*, and *bolina* standard, while here there is no doubt that the female Papilio has pulled the Pierine away from the usual Pierine standard, though it has in turn been pulled away from its own male. The male, it is true, belongs to a synaposematic group of its own, but the female has joined the stronger combination. The pull has been mutual between female Papilio and Pierine, and the association must therefore be Müllerian.

(2) Here is one more piece of evidence. We have seen that from the nature of the case the attraction (so to call it) in a Müllerian assemblage acts, or may act, in all directions, for each member of a Müllerian group is potentially both mimic and model.

It ought then sometimes to happen, if the Müllerian theory is correct, that although one dominant species, distinguished perhaps for its hardiness and distasteful qualities, may act as the centre of a group, influencing all the other members, yet that these other (subordinate) members of the group should show signs of having influenced each other, apart from the dominant species.

Does this ever happen? Certainly it does.

Limnas chrysippus, a Danaine, is one of these dominant forms, numerous in individuals, hardy, conspicuous, proved to be distasteful, and accompanied by mimics wherever it goes. Among its mimics in Africa are an Acræa, and a Lycænid (allied to our common blues). Now it is quite evident that there is a mimetic relation between the Acræa and the Lycænid apart from that which exists between them both and the Limnas. In short, they resemble each other in some respects more than either of them resembles the common model. Hence one or other of these two, or perhaps both, must be distasteful, and therefore there must be a Müllerian element in the whole group, if, indeed, it be not entirely Müllerian.

It has been pointed out by Prof. Poulton that many beetles, belonging to different families, are all in a sense mimics of the hymenopterous group of the Mutillidæ, and yet they have become assimilated to each other in non-Mutilloid points.

Facts of this kind prepare us for a further consideration of great importance, with which I shall conclude.

(3) We find that it is impossible to regard the mimetic assemblages of a given region as so many isolated groups. As a matter of fact, though there are certain dominant forms which act, so to speak, as centres of attraction, we often find that the mimetic forms constitute a nexus, models of the most dissimilar aspect being held together, as it were, by a kind of connection which runs from group to group, gradations from one group to another being formed in the most unexpected ways. From the nature of things this point is difficult to illustrate within the limits of a lecture like the present; a few examples may suffice.

Starting from a white Pieris of ordinary aspect like *P. phaloe*, we can pass by easy stages through *P. calydonia* ♀ and *P. demophile* ♀ into a well-marked distasteful group of which the Ithomiine *Aeria agna* is a good example. From *P. demophile* ♀ we can also pass through *P. viardi* ♀ to the pattern of *Heliconius charitonia*, or in yet another direction by way of *P. tithoreides* ♀ to *Heliconius atthis* and *Tithorea pavonii*. *P. calydonia* ♀, again, gives us a fresh starting point from which to proceed by way of *P. kiçaha*, *P. pandosia*, and *P. leptalina* up to a well-marked Ithomiine group typified by *Napeogenes inachia*. We have already seen how *P. locusta* ♂, which presents the Pierine characters of *P. phaloe* in an intensified form, comes into association with another group of Heliconii, while the same butterfly forms an early link in the chain

which leads up by easy gradations through both sexes of various species of Perrhybris (another Pierine genus) to the red, black, and yellow Müllerian assemblage we have already considered. From an intermediate stage in this latter series, exemplified on the undersurface of *Perrhybris lorena* ♀, we get a passage to yet another Heliconiine scheme of coloration, that shown by *H. aranea.* Here, then, we have groups centring round protected Heliconiines and Ithomiines of the most varied aspects, all held together and linked up with white butterflies of the ordinary Pierine facies by a network of almost imperceptible gradations.

As a final illustration, let me direct your attention to the series formed by *Papilio iphidamas* ♀, *Euterpe approximata, E. bellona, E. nigrina* (underside), and *Heliconius venusta.*

We have only to examine a gradated series like this to see how difficult it is to account for it on Batesian lines. There is the common aposeme, the yellow patch on the dark forewing, running right through; but if the Papilio is the model for all the rest, why should these Euterpes, which are Pierines, mimic a mimic (the Heliconius) instead of going to the model itself (the Papilio)? If, on the other hand, we regard the Heliconius as the model, we are met by exactly the same difficulty, only that it is reversed. Now we know that some at least of these intermediate forms are numerous in individuals, and as soon as the Müllerian principle is admitted we can see how easily forms protected by distastefulness can arrange themselves into a gradational series of this kind. For every distasteful form tends to protect other forms on each side of itself; hence the existence of these transitional stages is just what we should expect. This group represents in miniature what is everywhere to be found when we examine a tropical butterfly fauna from the point of view of mimicry, and I think we have here discovered the answer to an objection that met us at the outset, namely, the difficulty of accounting, on the principle of natural selection, for the existence of these intermediate forms, including the initial mimetic stages. Whether or no the difficulty is a real one in the way of the Batesian theory, in view of the Müllerian principle it is non-existent.

The comparison may perhaps be allowed between these mimetic groups, each with its own type of coloration, and the solar and stellar systems. Sometimes, as in the solar system, there is one central member of the group dominating the whole and influencing its attendant planets to an extent in comparison with which the force they themselves can exercise is insignificant. At other times, as in the systems of double and multiple stars, there are bodies more nearly equal in mass and importance bound together by mutual attraction into a single combination, where each one effectively controls and is controlled by the rest. Could we imagine irregular wanderers through cosmic space which from time to time get drawn within the limits of some established system, we might in them find an analogy to certain species which seem to hover on the outskirts of mimetic groups, undecided, as it were, whether to throw in their lot with one association or another.

What result have we been able to reach to-night? Starting from the fact, long recognised by naturalists, of the wonderful likeness borne to each other by certain insects of widely different affinities, we have found that the first rational explanation of the phenomenon was given by Bates, who nevertheless did not conceal from himself that his interpretation left many of the observed facts unaccounted for. The fertile suggestion of Fritz Müller went far to supply what was still wanting. Expanded by Meldola and by Poulton, accepted by travelled naturalists like Wallace and Trimen, the Müllerian generalisation has proved a powerful means of interpretation of many complicated relationships. We have seen reason for concluding that such rival attempts at explanation as those which allege affinity, or geographical and climatic conditions, as adequate causes for the phenomena before us, break down on serious examination; and we have applied the final test of arguing deductively from the premises, and finding, on a fresh appeal to the facts, that our results are in accordance with expectation.

This verification, we saw, is concerned with the three chief topics of (1) the interchange of characters, or diaposematism; (2) the influencing of subordinate members of mimetic groups by one another; and (3) the nexus of protected conspicuous forms which may overspread a whole zoological continent.

I think no one who has paid attention to the facts that have been before us can fail to recognise that here, as everywhere in organised nature, the principle of adaptation is paramount. No scientific explanation of adaptation that really meets the case has yet been offered except natural selection. Whatever bearing the principle of adaptation by selection may have on the question of the origin of species—I for one venture to think that it has a very important bearing—it is a principle which cannot in fairness be ignored.

In what has been said I have tried to be explanatory rather than controversial, though it has not been possible to avoid altogether points that have given occasion for dispute. Those who are conversant with the subject will know that many questions of interest have been left unnoticed; but I trust that in this survey, necessarily brief, I have said enough to show how much of biological importance and interest is involved in the really great subject of mimicry.

UNIVERSITY AND EDUCATIONAL INTELLIGENCE.

CAMBRIDGE.—Mr. R. C. Punnett has been re-elected to the Balfour studentship for one year from Michaelmas, 1907.

A grant of 50*l.* from the Balfour fund has been made to Mr. W. E. Agar in furtherance of his expedition to the Paraguayan Chaco.

A proposed change in the Previous Examination, which may be of far-reaching importance, will be voted on by the Senate next week. At the suggestion of the Board of Examinations, a paper on elementary heat and chemistry will be set in part ii. of the Previous Examination as an alternative to the papers on Paley's "Evidences" and elementary logic. The Board also proposes the substitution of a single combined paper on arithmetic and algebra for the present separate papers on these subjects in the same examination.

The Special Board for Mathematics has issued an important report with reference to the constitution of the board. Owing to the new regulations, the examiners and moderators will in future be nominated by the board. The representatives of the college on the board given them in past years by the nomination of the moderators will thus disappear. The board considers it advisable that there should be direct representation of the mathematical lecturers of the University and of the colleges; it is therefore suggested that two members be nominated each year at a meeting held of the lecturers in subjects for the mathematical tripos.

The reforms which the board of mathematics have introduced into the University in the last four years are numerous and far-reaching. They include a complete revision of the mathematical tripos, the recognition that the teaching of mathematics should be correlated with that of physics and engineering, the establishment of a qualifying examination in mechanical sciences, re-casting of the mechanical sciences tripos, and reforms in the mathematical special examination for the ordinary degree.

Dr. Hobson has been re-elected president of the Cambridge Philosophical Society. The new vice-presidents are Prof. J. J. Thomson and Mr. S. Ruhemann. The new members of the council are Prof. T. B. Wood, Prof. B. Hopkinson, Dr. Searle, and Mr. W. E. Dickson. Mr. H. F. Newall has been re-elected treasurer, and Mr. A. E. Shipley, Dr. E. W. Barnes, and Mr. P. V. Bevan secretaries.

OXFORD.—The Romanes lecture will be delivered by the Chancellor of the University, Lord Curzon, All Souls' College, on Saturday, November 2, at 2.30, in the Sheldonian Theatre. The subject of the lecture will be "Frontiers."